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Caloric Primary Rewards Systematically Alter Time Perception

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Human time perception can be influenced by contextual factors, such as the presence of reward. Yet, the exact nature of the relationship between time perception and reward has not been conclusively characterized. We implemented a novel experimental paradigm to measure estimations of time across a range of suprasecond intervals, during the anticipation and after the consumption of fruit juice, a physiologically relevant primary reward. We show that average time estimations were systematically affected by the consumption of reward, but not by the anticipation of reward. Compared with baseline estimations of time, reward consumption was associated with subsequent overproductions of time, and this effect increased for larger magnitudes of reward. Additional experiments demonstrated that the effect of consumption did not extend to a secondary reward (money), a tasteless, noncaloric primary reward (water), or a sweet, noncaloric reward (aspartame). However, a tasteless caloric reward (maltodexrin) did induce overproductions of time, although this effect did not scale with reward magnitude. These results suggest that the consumption of caloric primary rewards can alter time perception, which may be a psychophysiological mechanism by which organisms regulate homeostatic balance.

Public Significance Statement
Recent work has suggested that human time perception can be influenced by rewards. We performed a series of experiments to test whether different types of primary rewards, such as fruit juice, could alter time perception. We found that time was systematically underestimated after the consumption of some rewards, but only when they contained calories. This suggests that time perception changes based on our physiological state, which may play a role in the regulation of feeding behavior and decision making.

Keywords: time perception, interval timing, primary reward

Supplemental materials: http://dx.doi.org/10.1037/xhp0000418.supp

When dining at a restaurant, it can sometimes seem that the hungrier we are, the longer our meals take to arrive. In contrast, once we have eaten, time does not drag on nearly as much—even if our wristwatch measures the durations as equivalent. It seems that our perception of time depends on our physiological state, and in particular, the anticipation and consumption of rewards. Yet, the relationship between the anticipation and consumption of reward and time perception are not very well understood.

Laboratory studies have shown that humans' perception of time is dynamic—a varying approximation of objective "clock time"—and can be influenced by a range of factors including novelty, stimulus complexity, our actions, and the temporal properties of the environment (Eagleman, 2008; Wenke & Haggard, 2009; Wiener, Thompson, & Coslett, 2014). The dominant "pacemaker-accumulator" models of time perception (Church, 1984) generally seek to explain these effects via arousal (which speeds up the rate of a hypothetical pacemaker; Treisman, 1963) and attention (which restricts the accumulation of the pacemaker's "pulses"; Zakay & Block, 1998). For example, according to these models, during states of physiological arousal—for instance when body temperature is high (Wearden & Penton-Voak, 1995), or during life threatening situations (Stetson, Fiesta, & Eagleman, 2007)—the

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rate of the pacemaker is increased, and durations are overestimated.

Similar outcomes can also be seen after pharmacological manipulations of arousal, such as noradrenergic blockage (Rammsayer, Hennig, Haag, & Lange, 2001), and dopaminergic stimulation (Meck, 1983). In particular, dopamine agonists cause earlier responding in timing tasks, consistent with an overestimation of duration, while antagonists have the opposite effect (Buhusi & Meck, 2002; Lake & Meck, 2013). Previous research has noted a neurobiological overlap between time processing and reward processing (Bermudez & Schultz, 2014; Meck, 2014), as midbrain dopamine neurons are also well known to respond to reward, and reward expectancy (Schultz, Dayan, & Montaguem 1997). The involvement of dopamine in each case suggests that rewards might exert an effect on time perception, either pharmacologically (via dopamine), or psychologically (via arousal).

However, few studies have explicitly investigated the effect of reward on time perception in humans, or have only done so using secondary rewards, like money (Balcı, Wiener, Çavdaroğlu, & Branch Coslett, 2013), or food imagery (Gable & Poole, 2012), as opposed to primary rewards, like food or drink. For example, Gable and Poole (2012) found that the duration of images of appetizing food was underestimated compared with control images. They suggested that it may be adaptive for durations to be underestimated when anticipating rewards, as this may prolong reward seeking (Gable & Poole, 2012). From the perspective of a pacemaker-accumulator model, these findings cannot be explained by dopamine or arousal, which would cause the images to be overestimated. They are, however, consistent with an attentional effect: attention toward food-related imagery could restrict the amount of pulses accumulated in memory, resulting in underestimation.

A large body of research has investigated how the actual acquisition or consumption of reward might affect time perception in nonhuman animals, for whom time perception is commonly measured using conditioned responses. However, the overall result of these studies have been ambiguous (Bonem & Crossman, 1988). For instance, it has been reported, variously, that increasing the magnitude of reward causes timed responses to occur earlier (Galtress & Kirkpatrick, 2009), later (Blomeley, Lowe, & Wearden, 2004), or to undergo no change (MacEwen & Killeen, 1991). Others have found differences in the timing of the first response, but not the time of the highest response rate, or the timing of the last response (Ludvig, Conover, & Shizgal, 2007), which could potentially be interpreted as a change in decision criteria (i.e., a motivational change) rather than a change in perceived time. One study that explicitly examined the effects of different nutrients on time perception in rats found that carbohydrates caused later responses, while other nutrient compounds caused earlier responses (Meck & Church, 1987). The ambivalence of results from previous studies may therefore be a consequence of different types of primary reinforcement. Thus, despite considerable evidence that primary rewards can affect time perception, the direction and cause of this effect are unclear. It has also yet to been seen whether primary reward can affect time perception in humans, who can be explicitly asked to estimate time intervals.

Here we present five experiments, which directly tested how different primary and secondary rewards affect time estimation in humans. Our experimental paradigm used a novel variant of a temporal production procedure (Zakay & Block, 1997) in which participants made time estimations of half the duration of the waiting time during a delayed reward delivery. In the first experiment, rewards were different volumes of fruit juice, which constitutes a caloric primary reward with inherent biological value, often used in both human and nonhuman primate studies (McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; Schultz et al., 1997). Reward magnitude was cued on a trial-by-trial basis and delivered using a syringe pump. This procedure had the advantage that both the size of reward and the timing of reward consumption could be precisely controlled, and we could assess the effect of both previously consumed rewards and anticipated rewards of different magnitudes.

Although it does not provide direct physiological benefit, the rewarding value of money has been suggested to be a modern derivative of that of food (Briers, Pandelaere, Dewitte, & Warlop, 2006). Thus, in a second experiment we investigated whether secondary rewards also have an effect on time perception, using monetary rewards. In a third experiment, we addressed the possibility that orosensory stimulation alone can affect time perception, by using different volumes of calorie-free liquid (water), instead of fruit juice. Finally, the fourth and fifth experiments attempted to identify whether the effect of fruit juice was primarily dependent on its sweet taste or its caloric content. To do this, we used an aspartame solution (a sweet, noncaloric compound) in the fourth experiment, and a maltodextrin solution (a tasteless, caloric compound) in the fifth experiment.

General Method

Participants

All 125 participants were recruited via advertisement at The University of Melbourne, after reporting no dietary restrictions (fructose intolerance, diabetes, phenylketonuria and fluid imbalance). Participants were instructed to refrain from eating or drinking for 4 hours prior to the experiment to decrease satiety. All participants provided written informed consent. The study protocol for all experiments was approved by The University of Melbourne's Human Research Ethics Committee (no. 1441974).

Stimuli and Apparatus

Time perception was measured using a variant of a temporal production procedure (similar to a peak-interval procedure; Rakitin et al., 1998; Wearden & McShane, 1988; Figure 1b). In each trial, participants were first presented with a reward cue for 3 s that indicated different reward magnitudes, and the delay of reward delivery (either 4, 6, 8, or 10 s; Figure 1a). Following this, a black fixation cross appeared for the duration of the delay. Participants were asked to make a response at a target time that was half of the full delay (i.e., 2, 3, 4, or 5 s). When a response was registered, the fixation cross changed color to orange. Responding at half of the delay meant that the time of the response did not coincide with reward delivery, and ensured that the delivery of reward was precise and valid in respect to the cue. The use of a single response minimized the effect of excessive motor activity that multiple responses may have had on timing processes (Wenke

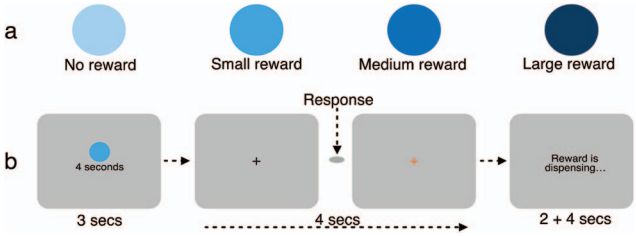

Figure 1. Time estimation task. Figure 1a: Reward cues; different hues coded for different reward sizes, the order of which were counterbalanced between participants. Figure 1b: Paradigm; participants were presented with a reward cue and the delay to delivery of the reward (e.g., 4 s). During the delay to delivery, participants made a response (indicated by a color change) approximating half the duration of the delay (the target time). At the end of the delay, the syringe pump was activated and appropriate reward was delivered over 2 s, followed by a 4-s intertrial interval. See the online article for the color version of this figure.

& Haggard, 2009). If participants missed a response, a text warning ("Please try to divide the delay in half") was displayed at the end of the delay, in addition to a standard message that indicated reward delivery ("Reward is dispensing . . ."). Regardless of whether participants missed the response or not, at the end of the full delay, the appropriate reward was delivered over a 2-s interval. Trials were separated by a further 4-s interval, which allowed for the swallowing of liquid rewards.

The Psychophysics Toolbox (Brainard, 1997) running on MATLAB 8.4 was used for stimulus presentation. A programmable syringe pump (SP210iw, World Precision Instruments, Sarasota, FL), controlled by MATLAB was used to deliver liquid rewards. Liquid from the two 150 mL syringes was merged into a single plastic tube and delivered to the participant via a disposable mouthpiece.

Experimental Procedures

Participants were first tested on the associations between the reward cues and the reward volumes. Any participant who failed to correctly categorize the rewards was asked to repeat this test until all rewards were correctly identified. Participants were instructed to avoid chronometric counting, to mitigate the effect of subvocal rhythm strategies, which can improve accuracy artificially (Rattat & Droit-Volet, 2012).

In each experiment, participants first completed an initial baseline time estimation task without reward cues and the delivery of reward, which allowed participants to familiarize themselves with the procedure. Participants then performed the main experimental task, including reward cues and reward delivery. Subsequently, participants performed a second baseline task without reward, which allowed the observation of any effects of cumulative reward consumption. In each of these task phases, every 20 trials participants were allowed to take a self-paced break. It is important to note that participants were told that the magnitude of reward received on each trial during the experiment was randomly chosen and entirely independent of their performance, allowing us to minimize motivational effects. For example, this prevented individuals from paying less attention to less valuable trials, which may have systematically effected their responses in ways unrelated to their percept of time. After completion of all experimental tasks, participants were debriefed.

Data Analysis

In each experiment, trials in which responses were missed, as well as trials with time estimations 2.5 standard deviations from the participants' mean estimation for that particular delay were excluded. Additionally, participants who missed more than 10% of all trials were excluded from analysis entirely, as we assumed these participants did not pay adequate attention to the task.

For each experiment, we first identified whether potential carry-over effects influenced time estimates on trial-by-trial basis. These included temporal carry-over effects (the influence of the delay experienced on the preceding trial), and decisional carry-over effects (the influence of the response of the previous trial; Wiener et al., 2014). We then identified whether there were general effects of reward, by comparing mean time estimates in the nonrewarded baseline tasks to those in the main experimental task.

Next, we provided a demonstration of the effect of the presence/absence of both anticipated and previously consumed reward independently, and unconditional on any other factors (excluding target time). We had to consider several constraints for this analysis approach. First, a model that coded reward magnitude as a continuous variable would constitute an analysis of covariance model, a key assumption of which is that the regression coefficients for the continuous variable are the same across categorical variables (i.e., target times). As our data exhibited the scalar property (variability that increases with target time), and Vierdordt's law (a central tendency effect), this assumption was violated. We therefore opted to treat reward magnitude as a categorical variable. This also allowed for the detection of any nonlinear effects (in pretesting, we found that individuals valued the liquid as a nonlinear function of its volume). Second, while we may have wished to model both anticipated and previously consumed reward simultaneously, the size of the combinatorial space of a repeated measures analysis of variance (ANOVA) design including both anticipated and previously consumed reward would be very large, and we could not reasonably have a sufficient number of trials to have balanced cells for each participant. This effectively prohibited us from using this approach. (However, the more powerful mixed-effects model below included both anticipated and previously consumed reward, as well as reward magnitude.) Given these constraints, we collapsed our data across reward magnitudes to identify whether the general presence of either anticipated or previously consumed rewards influenced time estimates, using data only from the main experimental task phase.

To determine whether these effects were dose-dependent, and to model both anticipated and previously consumed reward simultaneously, we then estimated a mixed effects panel regression model. This allowed us to assess trial-by-trial time estimates as a function of reward magnitude, and to control for the potentially obfuscating interplay of other relevant factors, while accounting for unobserved individual heterogeneity.

Where appropriate, Greenhouse–Geisser corrections were performed to account for violations of sphericity, and the correction factor values (ε) and original degrees of freedom are reported. Eta-squared effect-sizes are reported only for significant analyses. We used the statistical package "plm" for the mixed effects panel

regression model (Croissant & Millo, 2008) in R, which automatically omits variables with high collinearity. The Breusch–Pagan test of heteroskedasticity, and heteroskedasticity-consistent coefficients were also estimated using this package. Differences in all analyses were considered significant if $p < .05$.

Experiment 1 (Fruit Juice)

We first examined the potential effect of reward on time perception, by using an ecologically relevant primary reward. A variety of changes in decision making as a result of glucose consumption have previously been reported (Gailliot & Baumeister, 2007; Molden et al., 2012; Orquin & Kurzban, 2016), and previous nonhuman animal studies have found that carbohydrates affect time perception (Meck & Church, 1987). Caloric compounds also activate reward-related dopaminergic midbrain areas (Frank et al., 2008). Thus, we considered a caloric primary reward like fruit juice a likely candidate to affect time perception in humans.

Participants and Apparatus

Twenty-five right-handed participants were recruited for the first experiment (mean age, 20.3 years, range = 17–26; 17 female, 8 male). Participants were compensated with AUD 20 for their participation. In Experiment 1, rewards were different volumes of a commercially available apple juice (0.0, 0.5, 1.2, and 2.3 mL). Each combination of delay and reward was presented 10 times in pseudorandom order, resulting in a total of 160 trials. This led to a total consumption of 162 mL of liquid.

Results

In Experiment 1, of all trials collected, an average of 5 responses were missed per person (range = 0–26). A further average of 5.16 responses were excluded per person (range = 0–10) due to the standard deviation criterion (2.2% of all trials). No participants were excluded entirely.

Mean time estimates and time estimate variability. Time estimates increased monotonically with longer target times—one-way repeated measures ANOVA: $F(3, 72) = 522.57$, $p < .001$, $\varepsilon = 0.43$, $\eta^2 = 0.77$—implying that participants correctly followed the task instructions. The variability of time estimates also increased with target time—one-way repeated measures ANOVA: $F(3, 72) = 47.36$, $p < .001$, $\varepsilon = 0.72$ $\eta^2 = 0.33$—approximating the characteristic scalar property of timing. However, the coefficient of variation (CV; the standard deviation of the estimation divided by the mean estimation; Treisman, 1963) was significantly affected by target time—one-way repeated measures ANOVA, $F(3, 72) = 23.24$, $p < .001$, $\varepsilon = 0.74$, $\eta^2 = 0.14$—suggesting a violation of the scalar property (Lewis & Miall, 2009; Wearden & Lejeune, 2008).

Carry-over effects. As time estimates have previously reported to be influenced by both temporal and decisional carry-over effects (Wiener et al., 2014), we sought to identify whether these carry-over effects were present in our data. For each participant, we used linear regression to identify whether the target time or time estimate of the previous trial affected the time estimate of the current trial, while controlling for the target time of the current trial. A one-sample t test on the resulting individual beta coefficients revealed a significant effect of both previous target time, $t(24) = 4.33$, $p < .001$, $d = 0.87$ and previous time estimate, $t(24) = 6.35$, $p < .001$, $d = 1.32$, suggesting that both carry-over effects were present (see Table 1 for effect estimate).

Previous response ought to be a close function of previous target time, and thus these two variables ought to be correlated. To assess whether this might present an issue of multicollinearity in later analyses, we calculated variance inflation factors (VIF) in a simple linear model of target time, previous target time and previous response. Both previous target time and previous response had a VIF of 2.03, which indicated that multicollinearity was not problematic in terms of model estimation.

The general influence of reward on mean time estimates. Next, we tested whether the presence of reward had an effect on mean time estimates across all delays by comparing time estimates in the main reward task phase with time estimates made in the two nonrewarded baseline task phases (Figure 2a). We first standardized time estimates (mean estimate minus target time, divided by the standard deviation for each delay). As there was no significant difference between the first and second baseline task phases, $t(24) = -0.65$, $p = .521$, we averaged the standardized estimates from these. A two-tailed paired-samples t test revealed that time estimates were significantly overproduced in the main task phase compared with the baseline phases, $t(24) = 3.62$, $p = .001$, $d = 0.72$, indicating a general effect of the presence of reward on time estimates.

Effects of anticipated and previously consumed reward. We next identified whether rewards influenced time estimates within the main task phase. To do this, we collapsed across reward magnitudes and ran two two-way repeated measures ANOVAs, which included a factor for the target time and a binary factor representing the presence or absence of reward.

For the analysis of the effect of anticipated rewards (whether there was upcoming reward or not), the model revealed a significant effect of target time, $F(3, 72) = 358.43$, $p < .001$, $\varepsilon = 0.48$, $\eta^2 = 0.74$ (Figure 2b), but no significant effect of anticipated reward, $F(1, 24) = 1.46$, $p = .239$, nor an interaction of target time and anticipated reward, $F(3, 72) = 0.77$, $p = .514$.

For the analysis of the effect of previously consumed reward (whether reward was consumed at the end of the previous trial or not), we found a similar effect of target time, $F(3, 72) = 337.5$, $p < .001$, $\varepsilon = 0.46$, $\eta^2 = 0.73$, as well as a significant effect of previously consumed reward, $F(1, 24) = 13.57$, $p = .001$, $\eta^2 = 0.005$ (Figure 2c), but no interaction effect, $F(3, 72) = 1.5$, $p = .222$. Overall, this suggested that previously consumed rewards, but not anticipated rewards, was associated with overproduced time estimates within the main task phase.

Trial-by-trial effects of reward on time estimates. We next analyzed whether either the *magnitude* of anticipated reward or previously consumed reward had an effect on time estimates, or whether the observed effect was confounded by other factors. To this end, we estimated a mixed effects panel regression model, which accounted for participant heterogeneity as a random effect, as well as the fixed effects of (a) the *target time*, (b) temporal carry-over effects (*previous delay;* Wiener et al., 2014), (c) decisional carry-over effects (*previous time estimate;* Wiener et al., 2014), (d) *anticipated reward magnitude*, v) *previous reward magnitude*, and (e) possible satiety effects due

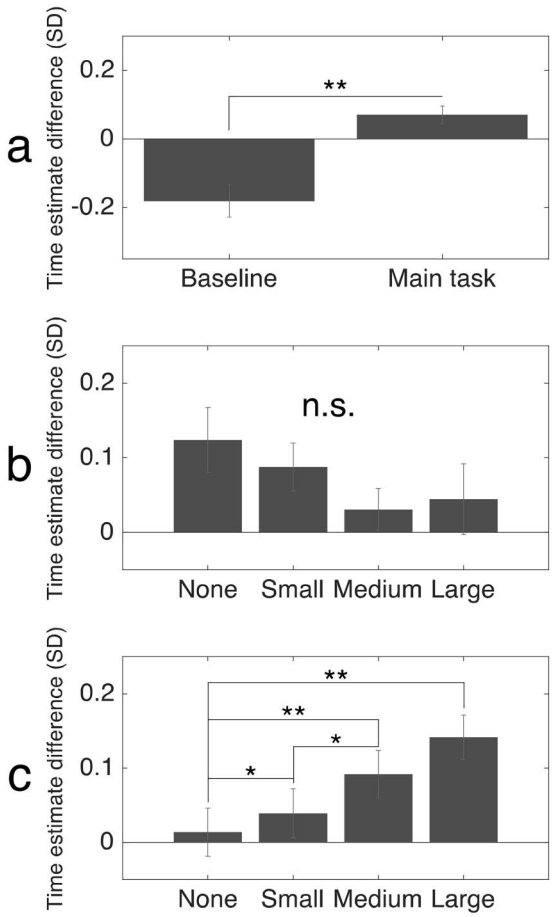

Figure 2. Effects of reward on mean time estimates in Experiment 1 (fruit juice). Figure 2a: Mean time estimates in main task versus baseline tasks. Time estimates are expressed as the difference between mean response and target time. Figure 2b: Effect of anticipated reward within main task phase; differences between reward conditions were nonsignificant (*ns*; $p > .1$). Figure 2c: Effect of previously consumed reward within main task phase; significant differences based on estimated marginal means of analyses of variance. Time estimates are expressed as standard deviations (the difference between mean response and target time, standardized by target time). Error bars: ± 1 *SEM*. * $p < .05$. ** $p < .01$.

to overconsumption (*total volume of consumed reward*). Given that the data displayed heteroskedasticity, Breush–Pagan test, $BP(14) = 302.89$, $p < .001$, heteroskedasticity-consistent coefficients were estimated.

The model revealed the expected significant effect of *target time*, *previous delay* (8 and 10 s), as well as *previous time estimate.* It is important to note that even when taking these variables into account, we found significant effects for the small, medium, and large *previous reward magnitudes* (see Table 1). The marginal effects of consumed rewards on response grew monotonically as their magnitude increased (0.053, 0.09, and 0.1 s, respectively), suggesting the effect was dose-dependent. No significant effects of *anticipated reward magnitude* were found. Overall, this model accounted for a substantial amount of variance in time estimates, $R^2 = .66$, $F(14, 3702) = 516.26$, $p < .001$.

Discussion

We found that time estimates were overproduced after consuming fruit juice, but that anticipating fruit juice rewards did not systematically affect mean time estimates. Furthermore, this effect was dose-dependent: larger volumes of fruit juice caused larger subsequent overproductions. Notably, we found that fruit juice consumption affected time estimates on a trial-by-trial basis, which suggests that the effect operated on a very short time scale. It is possible that this was due to anticipatory cephalic phase responses triggered by the sensation of nutrients in the mouth (Power & Schulkin, 2008). However, from this experiment alone, we are unable to determine whether this effect was specific to fruit juice, or whether other types of rewards would also be able to elicit changes in time perception.

Experiment 2 (Money)

In Experiment 2, we addressed the possibility that the effect reported in Experiment 1 would extend to secondary reinforcers (money). Although it does not provide direct physiological benefit, the rewarding value of money has been suggested to be a modern derivative of that of food (Briers, Pandelaere, Dewitte, & Warlop, 2006).

Participants and Apparatus

An independent sample of 25 participants was recruited (mean age, 21.4 years; range, 18–29; 13 female, 12 male, 2 left-handed). Different monetary amounts were used as rewards (0.0, 5, 15, and 30 cents). To retain incentive compatibility, participants in Experiment 2 were told that they would be paid a random amount up to AUD 20 during the task, but were guaranteed at least AUD 10 for their participation (however, rewards were predetermined such that

Table 1
Mixed Effects Panel Regression Estimates for Fruit Juice Experiment

	Dependent variable: time estimate	
Independent variable	Coefficient	Standard error
Mean intercept	1.874	0.096
Target time (3 s)	1.017***	0.056
Target time (4 s)	1.864***	0.092
Target time (5 s)	2.829***	0.130
Previous delay (6 s)	−.064	.034
Previous delay (8 s)	−.115***	.044
Previous delay (10 s)	−.172***	.061
Previous time estimate	.100***	.020
Anticipated reward (small)	−.021	.041
Anticipated reward (medium)	−.061	.033
Anticipated reward (large)	−.047	.054
Previous reward (small)	.053*	.024
Previous reward (medium)	.090**	.028
Previous reward (large)	.100**	.038
Total volume of consumed reward	−.0002	.0005
Observations		3,741
R^2		.661
Adjusted R^2		.654

* $p < .05$. ** $p < .01$. *** $p < .001$.

all participants were paid a final amount of AUD 20). Instead of tangible reward delivery, a message was displayed that indicated both monetary amount gained in that trial, and the total money won so far (see Figure S1 in the online supplemental material). All other task components were identical to Experiment 1.

Results

In Experiment 2, of all trials collected, an average of 3.2 (range = 0–12) were missed and a further average of 5.6 (range = 1–10) were excluded due to the standard deviation criterion (2.3% of all trials). No participants were excluded entirely.

Mean time estimates revealed the same general pattern of results as in Experiment 1 (for the analysis of carry-over effects, see supplementary information).

The general influence of reward on mean time estimates. We tested whether the presence of monetary reward had an effect on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phase, as in Experiment 1. There was no significant difference between the first and second baseline phases, $t(24) = -1.22$, $p = .233$, and we averaged the standardized estimates from both baseline phases. A two-tailed paired-samples t test revealed that time estimates were significantly overproduced in the reward phase compared with the baseline phases, $t(24) = 2.54$, $p = .018$, $d = 0.51$, suggesting a possible gross effect of reward on time estimates (see Table S1 in the online supplemental material for summary data).

Effects of anticipated and previously consumed reward. We next investigated whether monetary rewards influenced time estimates within the main task phase, using two two-way repeated measures ANOVA analyses identical to that in Experiment 1.

For the analysis of the effect of anticipated rewards, the ANOVA revealed a significant effect of target time, $F(3, 72) = 377.83$, $p < .001$, $\varepsilon = 0.49$, $\eta^2 = 0.74$, but no significant effect of anticipated reward, $F(1, 24) = 5.25$, $p = .998$, nor an interaction of target time and reward, $F(3, 72) = 0.19$, $p = .903$; see Table S2 in the online supplemental material for summary data.

For the analysis of the effect of previously consumed reward, we found a similar effect of target time, $F(3, 72) = 403.23$, $p < .001$, $\varepsilon = 0.47$, $\eta^2 = 0.77$, but no significant effect of reward, $F(1, 24) < 0.01$, $p = .968$, and no interaction effect, $F(3, 72) = 2.11$, $p = .106$ (see Table S3 in the online supplemental material for summary data).

Trial-by-trial effects of reward on time estimates. Finally, a mixed effects panel regression model identical to that in Experiment 1 was used to test whether there were complex interactions that may have masked any effects of reward. As the data displayed heteroskedasticity, Breush–Pagan test, $BP(14) = 426.2$, $p < .001$, heteroskedasticity-consistent coefficients were estimated. The model revealed effects of covariates similar to that of the first experiment (significant effects for *target time* and *previous time estimate*), but no significant effects of *anticipated reward magnitude* or *previous reward magnitude* (for all details, see Table S4 in the online supplemental material). This model accounted for a substantial amount of variance in time estimates, $R^2 = .7$, $F(14, 3764) = 628.1$, $p < .001$.

Discussion

Although we observed a general effect of the presence of reward on time estimates, different monetary amounts did not affect time estimates on a trial-by-trial basis. It is possible that the mere presence of reward in the main task phase caused overproductions of time as a result of differences in attention, rather than the economic value of the reward itself (see General Discussion). However, the reason for why monetary rewards did not exert trial-by-trial effects similar to fruit juice was likely due to the fact that money does not require actual 'consumption.' Whereas the consumption of primary rewards has immediate physiological value, any potential benefit derived from money occurs at an indefinite delay.

Experiment 3 (Water)

Having determined that the effect of fruit juice on time perception did not extend to secondary reinforcers, we hypothesized that the observed effect may generalize to tangible, physical rewards with similar orosensory properties. Thus, in Experiment 3, we used water as a reward, which constitutes a primary reward without caloric value.

Participants and Apparatus

A further 25 right-handed participants were recruited for a third experiment (mean age, 21.7 years; range, 18–32; 14 female, 11 male). Participants were compensated with AUD 20 for their participation. Different volumes of water were used as rewards (0.0, 0.5, 1.2, and 2.3 mL; Figure 1a). Each combination of delay and reward was presented 10 times in pseudorandom order, resulting in a total of 160 trials. This led to a total consumption of 162 mL of liquid. All other task components were identical to Experiment 1.

Results

In Experiment 3, of all trials collected, an average of 5.2 (range = 0–24) were missed, and a further average of 6.4 (range = 1–13) were excluded due to the standard deviation criterion (2.7% of all trials). No participants were excluded entirely.

Mean time estimates, time estimate variability, and temporal carry-over effects were again similar to those observed in Experiment 1 (see supplementary information).

The general influence of reward on mean time estimates. We tested whether the presence of water reward had an effect on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. As there was no significant difference between the first and second baseline phases, $t(24) = -1.62$, $p = .118$, we averaged these values. A two-tailed paired samples t test revealed that time estimates were significantly overproduced in the reward phase compared with the baseline phases, $t(24) = 2.53$, $p = .018$, $d = 0.51$, again suggesting a possible gross effect of the mere presence of reward on time estimates (see Table S1 in the online supplemental material).

Effects of anticipated and previously consumed reward. We next investigated whether water rewards influenced time esti-

mates within the main task phase, using two two-way repeated measures ANOVAs identical to those used in Experiment 1.

For the analysis of anticipated rewards, the ANOVA revealed a significant effect of target time, $F(3, 72) = 263.99$, $p < .001$, $\varepsilon = 0.53$, $\eta^2 = 0.67$, but no significant effect of anticipated reward, $F(1, 24) = 0.61$, $p = .441$, nor an interaction of target time and anticipated reward, $F(3, 72) = 1.35$, $p = .264$; see Table S2 in the online supplemental material.

For the analysis of previously consumed reward, we found a similar effect of target time, $F(3, 72) = 295.99$, $p < .001$, $\varepsilon = 0.53$, $\eta^2 = 0.69$, but no significant effect of previously consumed reward, $F(1, 24) = 0.49$, $p = .489$, and no interaction effect, $F(3, 72) = 0.52$, $p = .669$ (see Table S3 in the online supplemental material).

Trial-by-trial effects of reward on time estimates. We next analyzed whether either the magnitude of anticipated reward or previously consumed reward had an effect on time estimates on a trial-by-trial basis. Again, a mixed effects panel regression model was estimated to test whether there were complex interactions that masked any effects of reward, with variables identical to those used for the first experiment. As the data displayed heteroskedasticity, Breush–Pagan test, $BP(14) = 440.65$, $p < .001$, heteroskedasticity-consistent coefficients were estimated. The model revealed effects similar to that of the first experiment (significant effects for *target time, previous delay* and *previous time estimate*), but no significant effects of *anticipated reward magnitude* or *previous reward magnitude* (for details see Table S5 in the online supplemental material). This model accounted for a substantial amount of variance in time estimates, $R^2 = .64$, $F(14, 3654) = 469.92$, $p < .001$.

Discussion

While this experiment again demonstrated a general effect of the presence of reward on time estimates, we found that water did not affect time estimates on a trial-by-trial basis. Thus, it appeared that the orosensory qualities of liquid primary rewards were not sufficient to elicit the changes in time perception that we observed with fruit juice reward. It is possible that more specific, physiological characteristics of fruit juice were necessary to affect time estimates. This possibility was tested in the next experiment.

Experiment 4 (Aspartame)

In Experiment 4 and 5, we aimed to disassociate two prominent characteristics of the fruit juice reward used in Experiment 1, to determine whether its perceptual (sweetness) and alimentary (caloric) qualities alone were sufficient to influence time estimates. Given that the effect observed in Experiment 1 operated on a very short, trial-to-trial time scale, we speculated that the effect may be due to a cephalic phase response (an anticipatory metabolic response) triggered by the sensation of the liquid (Power & Schulkin, 2008), as nutrients could not be properly digested within this time. If this is the case, it is possible that the orosensory properties (e.g., sweetness) of the juice alone may act as a cue for future nutritional value, and thereby induce an effect. Thus, we first hypothesized that the sweet flavor of liquid alone might be sufficient to influence time estimates.

Participants and Apparatus

A further 25 right-handed participants were recruited for a fourth experiment (mean age, 20.3 years, range, 18–33; 14 female). Participants were compensated with AUD 20 for their participation. In Experiment 4, the liquid rewards were different volumes of a noncaloric, 0.02% aspartame solution (0.0, 0.7, 1.4, and 2.8 mL). Each baseline phase consistent of 32 trials, while main treatment task phase was 128 trials, resulting in a total consumption of 158.4 mL of liquid. All other task components were identical to Experiment 1.

Results

2 participants in Experiment 4 missed more than 10% of responses and were excluded from analysis. Of the remaining participants, an average 2.74 responses were missed per person (range = 0–11). A further average of 4 responses were excluded per person (range = 1–7) due to the standard deviation criterion (1.9% of all trials).

Mean time estimates, time estimate variability, and temporal carry-over effects were similar to those observed in Experiment 1 (see supplementary information).

The general influence of reward on mean time estimates. We tested whether there was a general influence of reward on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. As we found a significant difference between the first and second baseline phases, $t(22) = -3.01$, $p = .006$, $d = 0.63$, we compared the estimates in the main phase to each baseline phase separately. Time estimates were significantly overproduced in the main reward phase compared with both the first, $t(22) = 6.37$, $p < .001$, $d = 1.33$, and second nonrewarded baseline phases, $t(22) = 2.99$, $p = .007$, $d = 0.62$. This again suggested that the mere presence of reward affected time estimates (see Table S1 in the online supplemental material).

Effects of anticipated and previously consumed reward. We next identified whether artificially sweetened rewards influenced time estimates within the main task phase, using an identical analysis to that of Experiment 1.

For the analysis of anticipated rewards, the ANOVA revealed a significant effect of target time, $F(3, 66) = 420.1$, $p < .001$, $\varepsilon = 0.56$, $\eta^2 = 0.8$, but no significant effect of anticipated reward, $F(1, 22) = 0.1$, $p = .753$, nor an interaction of target time and reward, $F(3, 66) = 1.17$, $p = .329$ (see Table S2 in the online supplemental material).

For the analysis of previously consumed reward, we found a similar effect of target time, $F(3, 66) = 395.47$, $p < .001$, $\varepsilon = 0.51$, $\eta^2 = 0.8$, but no significant effect of previously consumed reward, $F(1, 22) = 0.03$, $p = .861$, and no interaction effect, $F(3, 66) = 0.22$, $p = .882$ (see Table S3 in the online supplemental material).

Trial-by-trial effects of reward on time estimates. We again used the same mixed effects panel regression model as for the previous experiments. These data again displayed heteroskedasticity, Breush–Pagan test, $BP(14) = 209.74$, $p < .001$, therefore heteroskedasticity-consistent coefficients were estimated. The model revealed the expected significant effect of target time, previous delay (10 s), as well as a small but significant effect for

total volume of consumed reward. The effect of previous time estimate was also significant. It is important to note that however, no significant effects of *anticipated*, or *previously consumed reward* were found (for details see Table S6 in the online supplemental material). Overall, this model accounted for a substantial amount of variance in time estimates, $R^2 = 0.68$, $F(14, 2770) = 423.15$, $p < .001$.

Discussion

The experiment using aspartame suggested that different magnitudes of artificially sweetened rewards had no effect on time estimates. However, despite equivalent ratings of subjective sweetness, compared with artificial sweeteners, caloric carbohydrates have a unique effect on taste and reward pathways in the brain, and more strongly active dopaminergic midbrain areas (Frank et al., 2008). Given that dopamine has been strongly associated with temporal processing (Bermudez & Schultz, 2014; Meck, 2014), it is possible that the caloric content of fruit juice was the key component necessary to affect time perception. This hypothesis was tested in the last experiment.

Experiment 5 (Maltodextrin)

Results from Experiment 4 suggested that sweet flavour alone was not sufficient to influence time estimates. An alternative possibility was that the caloric content of the fruit juice influenced time estimates. To test this, we performed a final experiment, using maltodextrin, a tasteless compound with a caloric content similar to that of glucose.

Participants and Apparatus

A further 25 right-handed participants were recruited (mean age, 22.7 years, range, 18–29; 18 female). Participants were compensated with AUD 20 for their participation. In Experiment 5, the liquid rewards were different volumes of a tasteless, 6.4% maltodextrin (DE 18) solution (0.0, 0.7, 1.4, and 2.8 mL). Each baseline phase consistent of 32 trials, while main treatment task phase was 128 trials, resulting in a total consumption of 158.4 mL of liquid. All other task components were identical to Experiment 1.

Results

1 participant missed more than 10% of responses and was excluded from the analysis. Of the remaining participants, an average 3.17 responses were missed per person (range = 0–17). A further average of 3.33 responses were excluded per person (range = 1–8) due to the standard deviation criterion (2.1% of all trials).

Mean time estimates, time estimate variability, and temporal carry-over effects were similar to those observed in Experiment 1 (see supplementary information, and Table 2 for carry-over effects).

The general influence of reward on mean time estimates. We tested whether there was a general influence of reward on standardized time estimates by comparing time estimates in the main reward phase with time estimates made in the two nonrewarded baseline phases, as in Experiment 1. As we found significant overproductions of target times in the second, relative to the first baseline phase, $t(23) = 3.11$, $p = .005$, $d = 0.0.64$, we compared the estimates in the main phase to each baseline separately. Time estimates in the main reward phase were significantly overproduced compared with those in the first nonrewarded baseline phase, $t(23) = 4.78$, $p < .001$, $d = 0.98$, but not compared with the second nonrewarded baseline phase, $t(23) = 1.41$, $p = .171$. This suggested a possible gross effect of reward on time estimates, which may have carried over into the second baseline task phase (see Table S1 in the online supplemental material).

Table 2
Mixed Effects Panel Regression Estimates for the Maltodextrin Experiment

Independent variable	Dependent variable: Time estimate	
	Coefficient	Standard error
Mean intercept	1.972	0.097
Target time (3 s)	1.071***	0.042
Target time (4 s)	1.916***	0.042
Target time (5 s)	3.068***	0.042
Previous delay (6 s)	−.086*	.046
Previous delay (8 s)	−.120†	.053
Previous delay (10 s)	−.144*	.067
Previous time estimate	.072***	.017
Anticipated reward (small)	.006	.042
Anticipated reward (medium)	.026	.042
Anticipated reward (large)	.048	.042
Previous reward (small)	.091**	.042
Previous reward (medium)	.075†	.042
Previous reward (large)	.070	.042
Total volume of consumed reward	−.0001	.0005
Observations		2,860
R^2		.671
Adjusted R^2		.662

† $p < .1$. * $p < .05$. ** $p < .01$. *** $p < .001$.

Effects of anticipated and previously consumed reward. We next identified whether tasteless, caloric rewards influenced time estimates within the main task phase, using an identical analysis to that of Experiment 1.

For the analysis of anticipated reward, the ANOVA revealed a significant effect of target time, $F(3, 69) = 480.92$, $p < .001$, $\varepsilon = 0.54$, $\eta^2 = 0.77$, but no significant effect of anticipated reward, $F(1, 23) = 0.08$, $p = .787$, nor an interaction of target time and anticipated reward, $F(3, 69) = 0.27$, $p = .847$ (see Table S2 in the online supplemental material).

For the analysis of previously consumed reward, we found a similar effect of target time, $F(3, 69) = 492.45$, $p < .001$, $\varepsilon = 0.51$, $\eta^2 = 0.8$, and the effect of consumed reward closely missed the significance threshold, $F(1, 23) = 3.51$, $p = .074$, $\eta^2 = 0.004$. There was no interaction effect, $F(3, 69) = 1.32$, $p = .274$; see Table S3 in the online supplemental material.

Trial-by-trial effects of reward on time estimates. Again, we applied the mixed effects panel regression model used in the preceding experiments. These data again displayed heteroskedasticity, Breush–Pagan test, $BP(14) = 242.3$, $p < .001$, therefore heteroskedasticity-consistent coefficients were estimated. The model revealed the expected significant effect of target time, previous delay (8 and 10 s), as well as a significant effect of previous time estimate. No significant effects of anticipated reward

magnitude were found. The model also revealed a significant effect of the previously consumed 'small' reward. Moreover, both the 'medium' and 'large' previously consumed rewards narrowly missed the significance threshold (for details see Table 2). Overall, this model accounted for a substantial amount of variance in time estimates, $R^2 = 0.67$, $F(14, 2822) = 411.6$, $p < .001$.

In summary, the mixed effects panel regression model suggested a small effect of previously consumed, but not anticipated reward magnitude on time estimations. Consumption of reward in the previous trial was associated with later time estimates, but the marginal effects of consumed rewards relative to baseline were similar for each reward magnitude (0.09, 0.08, and 0.07 s, respectively).

General Discussion

In the present study, we tested whether the anticipation and consumption of different primary rewards and one secondary reward could alter time estimations. We found that for a range of suprasecond delays, time estimates were overproduced after the consumption of fruit juice on a trial-by-trial basis in a dose dependent manner. We also observed a marginally significant effect of a caloric maltodextrin solution on time estimates, but this did not appear to be dose dependent. These results were robust when taking into account other factors that are known to influence time estimations, such as the previously experienced delays and the previous responses (Wiener et al., 2014).

We also showed that the effect of reward consumption on time estimates did not extend to money (a secondary reward), water (a noncaloric, tasteless primary reward), or aspartame (a noncaloric sweet reward), although we did find a general effect of the presence of reward in all experiments. Anticipating rewards did not alter time estimates for any of the tested rewards.

These results contribute to previous demonstrations of the influence of contextual factors on time perception, and in particular those involving physiological factors (Campbell, Murphy, & Boothroyd, 2001; Gable & Poole, 2012; Wearden & Penton-Voak, 1995). Our results are consistent with those from nonhuman animal studies that have observed overproductions of time as a result of carbohydrate consumption (Meck & Church, 1987), as well as human neuroimaging studies that have linked homeostasis and interoception to time perception (Craig, 2009; Wittmann, van Wassenhove, Craig, & Paulus, 2010).

The effects in our experiments were found to be exclusive to reward consumption (experienced utility), and not reward anticipation (utility from anticipation; Loewenstein, 1987). This contrasts with previous findings such as the underestimation of time for images of prospective food rewards (Gable & Poole, 2012), which are somewhat equivalent to the reward cues in our task. However, individuals have a strong conditioned physiological response to the visual characteristics of food (Nederkoorn, Smulders, & Jansen, 2000), and thus, compared with the symbolic reward cues in our task, the images of food in the previous study may act in a way more similar to actual reward receipt. Nevertheless, it is somewhat surprising that the anticipation of rewards did not alter time estimates, as dopamine neurons are well-known to respond to expected reward, particularly when the relationship between a cue and reward receipt has been established (Schultz et al., 1997).

In addition to the effects of specific rewards on time perception, we also found that time estimates were affected by other variables in the previous trial. Previous durations (i.e., the target time of the previous trial) exerted a contrastive effect, such that responses were negatively correlated with the previous duration of the previous trial. Additionally, previous responses exerted an assimilative effect, such that responses were positively correlated between trials (taking into account the target time of each trial). These findings are in line with previous research that has reported dissociable effects of previous decisions and previously perceived durations on temporal discriminations for subsecond intervals (Wiener et al., 2014). However, in our experiment we used a temporal production task and suprasecond delays, and thus we extend these previous findings to a different time estimation paradigm and a larger scale of timing. Note, however, that the observed effect of previously consumed rewards remained robust despite the influence of preceding context.

In all five experiments, we found that the mere presence of reward caused overproductions of time, relative to nonrewarded baseline tasks that were in all other ways identical. One possible explanation is provided by pacemaker-accumulator models of time perception (Church, 1984). The addition of each of the rewards may have captured attentional processes, which would attenuate the accumulation of pacemaker signals (Zakay & Block, 1998), leading to an underestimation of the rate of time passing, and therefore overproductions of the target time. Thus, this general effect may not have been due to the rewarding qualities of each of the tested substances alone, but rather due to the inclusion of an additional, potentially distracting factor which competed with executive resources. Indeed, other time production experiments that have introduced concurrent tasks find similar effects (Brown et al., 2013). The visual stimuli in Experiment 2 (which indicated monetary amount but had no physically rewarding properties) still caused general underestimation effects between task blocks, which supports the idea that the mere inclusion of irrelevant information can alter time estimates (Schweitzer, Trapp, & Bar, 2017). A future experiment employing an explicitly nonrewarding stimulus could provide evidence for this interpretation.

The receipt of money, water, and aspartame, however, did not affect time estimates within the main task phase. As a secondary reward, money does not hold immediate physiological value, and while water and aspartame have similar immediate orosensory characteristics to fruit juice and maltodextrin, they lack the caloric, nutritional content that is present in both. Thus, the caloric content of the fruit juice is a strong candidate for the source of its effect on time perception. Previous research has identified that the caloric and taste components of food elicit neural activity in different brain regions, and that caloric compounds tend to more strongly activate classic dopaminergic midbrain areas, relative to artificial sweeteners (Chambers, Bridge, & Jones, 2009; Frank et al., 2008; Smeets, Weijzen, de Graaf, & Viergever, 2011; Tellez et al., 2016). Given the theoretical accounts of dopamine activity accelerating the rate of timing passing (Buhusi & Meck, 2002; Lake & Meck, 2013), we might have expected that caloric compounds would result in underproductions of the target time, which is not what we observed. However, more recent optogenetic studies have shown that the direct activation of dopamine neurons can actually lead to overproductions of time (Soares, Atallah, & Paton, 2016). This evidence provides an alternative explanation for our results,

consistent with increased dopaminergic activity after calorie consumption. From a psychological perspective, this explanation of our results relies on the assumption that the detection or processing of calories recruits attentional resources, which could impede the accumulation of pacemaker signals (Lake & Meck, 2013).

Notably, the effect of the maltodextrin solution was only marginally significant, and while the estimates of effect size were comparable to that of fruit juice, increasing the volumes of maltodextrin did not induce increasing overproductions of time. There are a number of possible explanations for this. First, while maltodextrin has a comparable glyclemic index to glucose, it does not decrease hypothalamic activity to the same degree (Smeets, de Graaf, Stafleu, van Osch, & van der Grond, 2005). Similarly, it does not induce a rise in insulin as rapidly as glucose (Smeets et al., 2005). Moreover, fruit juice contains a complex combination of nutrients, the physiological interactions of which may have complicated effects. For instance, the combination of glucose and fructose in ecological ratios may be important. Alternatively, it is also possible that perceptual sweetness can enhance the detection of calories, and thus a combination of these two qualities may be necessary to elicit reliable, dose-dependent changes in time perception.

We note that the trial-by-trial effect of fruit juice on time estimates operates on a rather short time scale, and thus is unlikely to result from the absorption or metabolism of nutrients, as has been previously suggested (Meck & Church, 1987). However, the mere orosensation of caloric compounds (compared with artificially sweetened solutions) appears to affect behavior in other domains including exercise physiology (Chambers et al., 2009; de Ataide e Silva et al., 2014; de Salles Painelli, Nicastro, & Lancha, 2010; Jeukendrup & Chambers, 2010; Rollo & Williams, 2011) and self-control (Molden et al., 2012), which has led to the proposal that there exists an unidentified class of oral carbohydrate receptors which anticipate the actual digestion of calories. Granted that caloric content can affect time perception as our results suggest, one possibility, which we did not test directly in this study, is that this effect operates via a similar mechanism. A similar effect has precedence in the sports physiology literature (Chambers et al., 2009; Jeukendrup & Chambers, 2010), where differences in the concentration and duration of carbohydrate exposure may alter the effect on motor performance (Devenney, Collins, & Shortall, 2016). It would be valuable for future research to address whether such differences also alter the effect observed in our experiment.

Given the small timescale of the effect, we might have expected that the underestimations induced by caloric rewards would have lessened at longer target times. However, we did not observe any interaction effects of target time and previously consumed reward. This may point to a simple effect of reward that does not differ as a function of delay. Alternatively this may also be explained by either the limited range of short target times employed here, or by the limited range of reward magnitudes. However, the lack of an interaction effect suggests that the effect may last up to 12 s after consumption of calories (a 4-s intertrial interval plus 3 s for cue presentation followed by a 5-s target time). Future studies may be able to investigate this further, for example by having longer trials, or by testing whether substantially larger rewards might have stronger effects.

We observed a dose-dependent effect of fruit juice on time perception. One implication of this result is that consumption on a larger scale may impact decision making behavior beyond simple perceptual judgments. For example, glucose consumption has been shown to decrease the perceived angle of hill slants, suggesting that spatial perception is a function of the relative energy resources required for locomotive effort (Schnall, Zadra, & Proffitt, 2010). Given that there are metabolic costs associated with passive waiting, increased energy resources may decrease the perceived duration of time—as we observe in our experiment—and lead to altered decision making. Delay discounting (Loewenstein, Read, & Baumeister, 2003), and foraging (Stephens & Krebs, 1986), are both decision-making processes that specifically involve a representation of time. Recent research has demonstrated that glucose consumption can decrease discount rates (compared with artificial sweeteners; Wang & Dvorak, 2010). Similarly, it has been shown that the "hunger hormone" ghrelin decreases patience (Anderberg et al., 2015). These studies recapitulate the notion that patience should be enhanced as organisms become sated, as the requirement for nutrition is less urgent. Our results are consistent with this notion, and provide a plausible psychophysiological explanation for the above effect. Further research may be able to identify whether other nutritional compounds (e.g., proteins, fats) have similar effects on time perception.

In conclusion, our study suggests that time perception changes as a result of the consumption of fruit juice rewards, and that larger amounts of consumption lead to larger overproductions of time. In showing that maltodextrin has a similar, but less extensive effect, our study suggests that caloric content is the critical driver of the effect. This highlights the role that homeostatic factors have in altering our fundamental perception of the world, and suggests that the consumption of primary rewards may have an underestimated, but important influence on time-dependent behaviors.

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